42. The Deinocephalia, an Order of Mammal-like Reptiles.

By D. M. S. Watson, M.Sc., F.Z.S., Lecturer on Vertebrate Palæontology in University College, London.

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(Plates IV., V.* & Text-figures 1–18.)

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In 1851 Andrew Geddes Bain forwarded to the Geological Society of London a series of fossil bones from the River Gamka, Great Karroo, South Africa, which he recognised as different from all the others he had collected.

These bones—a femur, humerus, ilium, vertebræ, and portions of skull-bones—were the first fragments of a Deinocephalian to be found in South Africa. Many years before, however, the copper mines of the Ural Mountains had yielded fragmentary bones which were described by Kutorga; these are now known to belong to Deinocephalians. The first South African type to be described was *Tapinocephalus atherstonei* Owen, the snout of which was excellently figured and shortly described in the 'Catalogue of Fossil Reptiles of South Africa in the British Museum.' In this work Owen described some vertebræ and limb-bones belonging to Deinocephalia, but by a confusion in localities attributed many of them to *Pariasaurus*. Some years later Owen described the very fragmentary remains of *Titanosuchus*.

* For explanation of the Plates see p. 786.

The first account of a skull which was in any way complete was written by H. G. Seeley on material of *Rhophalodon* and *Deuterosaurus* from the Urals. Subsequently the same author described a good skull belonging to the South African Museum as *Delphinognathus conocephalus*.

Except for purely systematic descriptions by Broom of four new genera and five new species founded on most unsatisfactory material, nothing further was published till, in 1909, this author gave a short and, as it has proved, somewhat inaccurate account of two skulls in the British Museum collected by Prof. Seeley. Subsequently Broom published a much better account of the type skull of *Delphinognathus* and brief descriptions of several new genera, one of which gave a complete knowledge of the lower jaw.

Finally, Haughton has published a short account of a large skull referred, perhaps correctly, to *Tapinocephalus atherstonei*.

The British Museum (Natural History) contains a large amount of Deinocephalian material in the form of more or less fragmentary skulls and small associated sets of bones. From this it is possible to get some idea of the form and structure of a member of the group, and to give a nearly complete account of the morphology of the skull.

The description of the Tapinocephaloid skull now given is founded on the following material:—

I. R. 1705. The type skull of *Tapinocephalus atherstonei*, represented by the right side of the occipital region up to the orbit, the left supraorbital region, and the anterior part of the face.

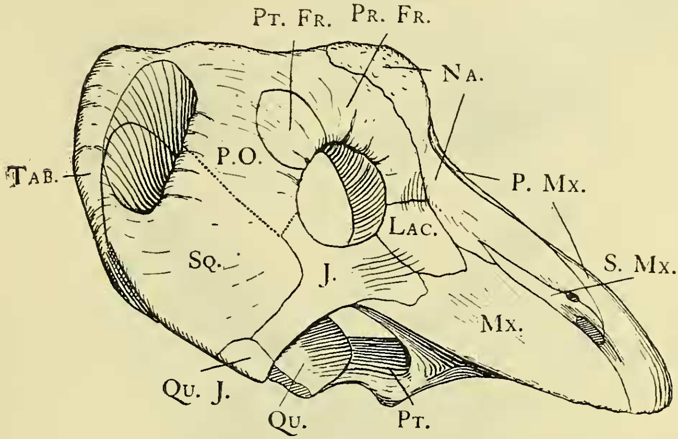
II. R. 3594. The skull already described by Broom as *Tapinocephalus atherstonei* which really belongs to a new genus (Pl. IV. and text-figs. 1–4).

This skull has lost the basioccipital condyle and the left quadrate region. It is very slightly distorted by pressure but otherwise is very well preserved, having been completely freed from a most intractable matrix by Mr. R. Hall, of the British Museum. When Dr. Broom described it, the whole outer surface was covered with a thin layer of matrix which has proved to be readily removable, so that all the sutures of the face are clearly and definitely shown; most of those figured by Broom are wrong.

III. R. 3596 is a specimen in the Seeley collection from De Cypher, Gouph, consisting of a skull (text-figs. 5–7) from which the face in advance of the prefrontal had fallen away before fossilisation, the two dentaries, with some limb-bones and vertebræ. Although also referred by Broom to *Tapinocephalus*, this skull is generically distinct not only from this type but also from R. 3594.

IV. 49385 is a specimen, Q of T. Bain's collection, from Warm Bad, Gouph, which consists of the posterior part of the skull, lacking most of the quadrates, and the anterior part of the face, which is only connected with it by documentary evidence (text-figs. 8, 9). This specimen also represents a new genus.

Text-figure 1.



Mormosaurus seeleyi, gen. et sp. n.

R. 3594 B.M.N.H. Type-skull. Right lateral aspect*, × 1/6

J., Jugal; LAC., Lachrymal; MX., Maxilla; NA., Nasal; P.O., Postorbital; PT. Pterygoid; PT.FR., Postfrontal; PR.FR., Prefrontal; P.MX., Premaxilla; QU., Quadrate; QU.J., Quadratojugal; S.MX., Septomaxilla; SQ., Squamosal; TAB., Tabulare.

Although these skulls belong to four different genera, they agree so closely in their fundamental architecture that I have used them all in the following description, which is, however, founded as far as possible on R. 3594, from which the account of the face and palate are almost wholly drawn.

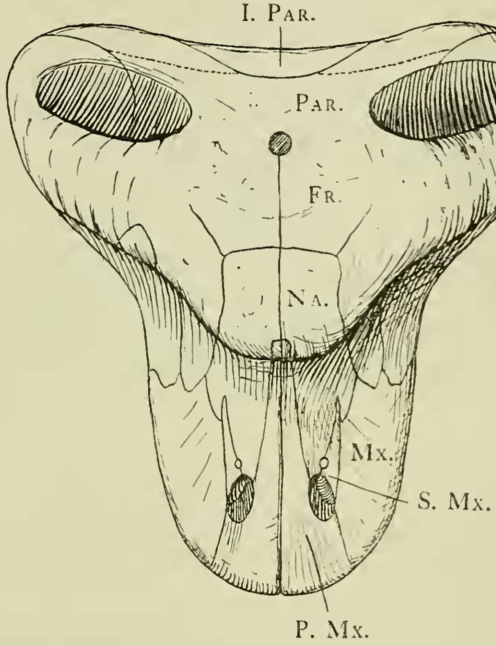
[This method I hold to be perfectly legitimate; it is as if we were describing the characteristic structure of a mammal's skull from incomplete but complementary skulls of a bear, a dog, and a cat.]

The Tapinocephaloid skull (text-figs. 1–9) has an extraordinarily large and massive cranial portion beside which the often sharply marked off face seems rather feeble. The whole of the bones on the dorsal surface of the postorbital region fuse together and thicken probably throughout the animal's life, until as much as

* Skulls from the Karroo of South Africa are usually distorted; in many cases this is of the nature of a simple sheer, which is very easily corrected in making drawings. In the figures of this paper this correction has been made, and each side is restored by comparison with the other. Nothing is introduced into them without clear evidence on at least one side. All the figures are projections and not perspective drawings.

fifteen centimetres of solid finely cancellar bone may be formed over the brain. The bones of the face, although they may be two centimetres thick, never fuse, and were readily disarticulated in the adult skull.

Text-figure 2.



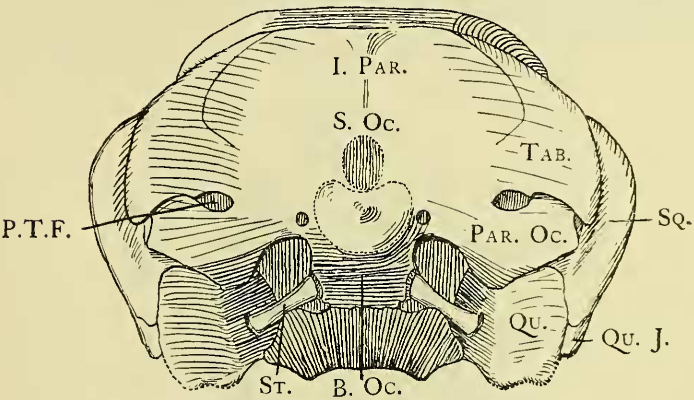
Mormosaurus seeleyi. Dorsal aspect of the type-skull, × ⅙.

Reference-letters as before, with :—Fr., Frontal ; I.Par., Interparietal ; Par., Parietal.

The whole occipital and otic region of the skull (text-figs. 3, 7) has fused into a mass of bone in which no sutures are visible in the material at my disposal. On the whole this region is very like the corresponding part of *Lystrosaurus* which I have already described. It forms a thick, vertically placed plate of bone pierced through the middle by the relatively small brain-cavity. This is throughout higher than wide, and has not been cleaned in any specimens ; fractures, however, show that it possessed the characteristic Therapsid character of having the large opening to the vestibule placed very low down in the skull. The floor of the brain-cavity rises considerably towards the front.

The basioccipital condyle (text-figs. 3, 4, 7) is single, large, and slightly pedunculate (R. 3596) ; it has a slight median depression representing the notochordal pit. Below the condyle, the basioccipital forms a vertical area, which may be very high and wide (text-fig. 7) (R. 3596) or comparatively small. The sides of this area must be formed by the paroccipitals for some distance, as the fenestræ ovales lie at the sides well below the condyle. The corresponding flat area in front is formed by the basisphenoid. There are no distinct tubera basisphenoidalia, or basipterygoid processes, but the posterior ends of the pterygoids articulate and indeed fuse with the lower margin of the vertical area. From

Text-figure 3.



Mormosaurus seeleyi. Posterior view of the type-skull, × $\frac{1}{6}$.

Reference-letters as before, with :—B.Oc., Basioccipital ; Par.Oc., Paroccipital ; P.T.F., Post-temporal fossa ; St., Stapes.

between them the narrow parasphenoid rises as a vertical plate, separated from much of the front of the basisphenoid by the deep, short notch which is the pituitary fossa. This fossa is bounded laterally by very low ridges which run upwards on the vertical anterior face of the basisphenoid until they terminate in low processes which are the processi anteriores prootici. The prootic of course contributes to the fenestra ovalis, above which it is perforated by the aquæductus fallopii for the VIIth nerve.

The otic and supraoccipital regions of the skull are in contact with the following bones :—

The upper outer corner of the posterior face of the large paroccipital process with the tabulare.

The outer end and front face of the paroccipital process with the squamosal.

The lower part of the front face of the paroccipital process with the quadrate.

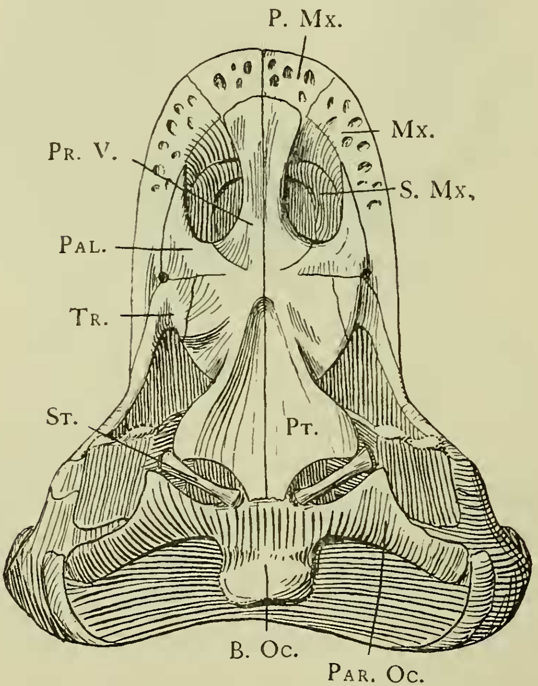
The posterior surface of the supraoccipital region is covered by the interparietal and tabulares. Its upper margin (and part of the front face ?) by the parietal (and postorbital ?).

The parasphenoid (text-fig. 9, Par.Sp.), as has been described above, rises from the front face of the basisphenoid. It is very short antero-posteriorly and rises nearly vertically in the skull about to the level of the anterior inferior process of the prootic; its upper end is then split and receives the lower end of the ethmoid.

The ethmoid is a remarkable bone extremely like that of *Endothiodon*.

Its lower border is clasped by the split upper edge of the parasphenoid, from which it rises as a narrow vertical plate; in front this is continued to the roof of the skull, but behind it

Text-figure 4.



Mormosaurus seeleyi. Palatal aspect of the type-skull, × ⅙.

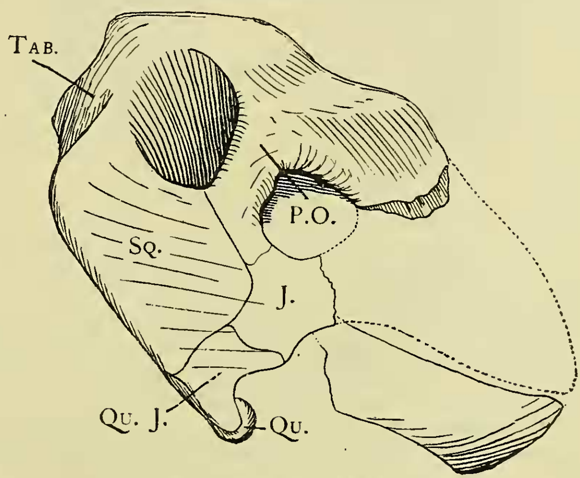
Reference-letters as before, with:—Pr.V., Prevomer; Pal., Palatine; Tr., Transverse bone.

splits into two branches which rise to the frontals and leave between them a small cavity for the olfactory lobes of the brain. The nasal nerves leave by a pair of openings between the median septal part of the ethmoid and the rest of that bone. The ethmoid is received in a groove on the lower surface of the frontals (and parietals?) and extends so far backwards that it nearly, if not quite, touches the supraoccipital.

The interparietal (I. Par.) is a flat bone entirely on the back of the skull, where it overlaps the supraoccipital below and the tabulares at the sides. The rest of its front face is in contact with the hinder ends of the greatly thickened parietals.

The tabulare (Tab.) is a large bone forming a good deal of the occipital surface. It is wedged in between the postorbital and interparietal (R. 3594), and passes outwards above the post-temporal fossa to touch the outer end of the paroccipital. The outer part of its front face is in contact with the squamosal, and its thick outer border joins with this bone to make a distinct auditory meatus.

Text-figure 5.



Pnigalion oweni, gen. et sp. n.

Right lateral aspect of the type-skull. R. 3596 B.M.N.H. × $\frac{1}{6}$.

Reference-letters as before.

The squamosal (Sq.) is a large bone which has a powerful articulation with the end of the paroccipital process; above the articulation a strong ramus runs inwards along the front face of the tabulare to overlap the postorbital. Immediately to the outside of its articulation with the paroccipital process the bone overlaps the upper end and some of the posterior surface of the quadrate. Finally, the bone is completed by a powerful ramus which forms part of the outer wall of the skull, articulating with the lateral border of the quadrate and ending in suture with the quadrato-jugal, jugal, and postorbital.

None of the specimens shows clearly all the sutures bounding the parietal, but it is certain that the two bones met in a median suture which is only interrupted by the long cylindrical tunnel which forms the large pineal foramen.

The posterior border of the bone is covered by the interparietal. Anteriorly it must meet the frontal, but the suture is never visible. The lateral border is completely covered by the postorbital.

The excessive thickness of the bones makes them come into contact with the upper border and anterior face of the supraoccipital.

The postorbital (P.O.) is a large and very remarkable bone. It forms the massive bar behind the orbit, and has a very long suture with the squamosal in the zygomatic arch below the temporal fossa.

Above the orbit in R. 3594 it meets the small post-frontal, but in that specimen on its lower surface (on the right side) it can be distinctly seen to join the prefrontal in a long suture running inwards nearly to the middle line. The extremely thick and massive bone then meets the parietal and covers the whole of its outer surface, sending out a process in contact with the front face of the interparietal and tabulare to be finally covered by the tip of the parietal ramus of the squamosal, so that the temporal fossa is entirely bounded by these two bones.

The sutures between the postorbital, frontal, and prefrontal are not visible on the outside of the skull.

The postfrontal (Pt.Fr.) is a very small bone forming a small part of the orbital margin and entirely surrounded by the prefrontal and postorbital (R. 3594).

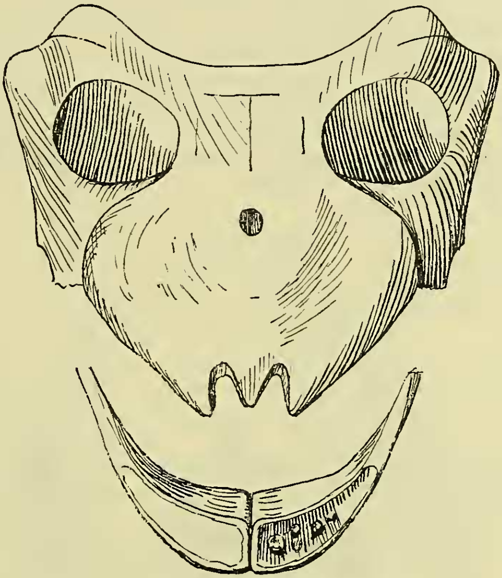
The prefrontal (Pr.Fr.) is a very massive bone forming the front upper quadrant of the orbital margin. On its ventral surface it has a long suture with the postorbital and likewise joins the postfrontal, frontal, nasal, and lachrymal.

The lachrymal (Lac.) (R. 3594) is a small bone forming the front of the orbit and articulating with the prefrontal, nasal, maxilla, and jugal. There is no lachrymal foramen.

The nasal (Na.) (R. 3594) is a large bone which plays a great part in the structure of the face. The two bones are in contact in the middle line posteriorly, where they are very thick, but their thinner anterior portions are separated by the very long internarial processes of the premaxillæ. The outer border of the nasal has a suture with the prefrontal, lachrymal, maxilla, and septomaxilla, and is entirely excluded from the nostril by the latter bone. The visceral surface of each nasal has a sharp ridge, the two together forming a groove for the olfactory nerves.

The premaxilla (P.Mx.) of R. 3594 is a very remarkable bone. It has a suture with its fellow, with which it forms the rounded extremity of the snout. Its tooth-bearing margin is short and wide, and its inner edge forms part of the anterior border of the posterior naris. Medial to this opening it sends back a process along the upper surface of the prevomer. The dorsal surface of this process forms a floor to the anterior part of the nasal cavity, and its outer border is in contact with the septomaxilla. The outer side of the premaxilla has a powerful articulation with the maxilla. In R. 3594 the facial part of the bone is continued upwards by a long and slender internarial process which separates the nasals for a great distance.

Text-figure 6.



Pnigalion oweni. Type-skull, dorsal aspect, × $\frac{1}{6}$.

The maxilla (Mx.) is a bone with few remarkable features; in front it joins the premaxilla, and thence backwards forms a large area of the face. It is completely excluded from the border of the external naris by the septomaxilla, with which in R. 3594 it has a long suture. In this specimen it then has a short contact with the nasal and is finally terminated by sutures with the lachrymal and jugal. On the palate the maxilla is only represented by its wide tooth-bearing edge and forms part of the border of the choana; for the rest of its length it is in contact with the palatine and transverse bones.

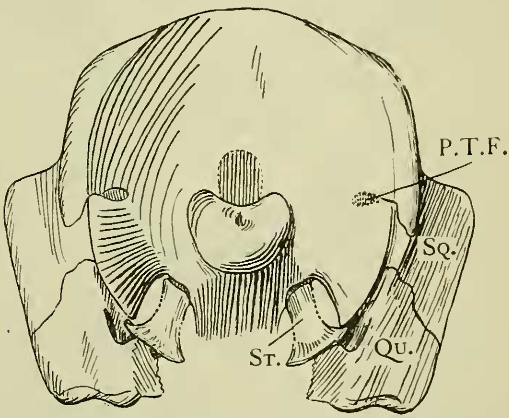
The septomaxilla (S.Mx.) is a variable bone in Tapinocephaloids. In R. 3594 it has an internarial part which unites by suture with the premaxilla to form a floor to the nasal cavity; it then sends back a large facial part which forms the whole of the posterior border of the nostril and separates the nasal and maxilla for a long distance; it is in contact with the maxilla throughout its length, but is separated from the nasal just behind the nostril by a foramen about a centimetre long and ·5 cm. wide.

In 49385 the septomaxilla is entirely within the nostril, in which it forms an irregular curved plate, having a suture with the premaxilla and forming a rudimentary floor to the nasal cavity. Its outer border is in contact with the maxilla except for a small foramen of irregular shape (text-figs. 1, 2).

The jugal (J.) is a comparatively small bone which forms about a quarter of the orbital margin: in front it terminates in sutures with the lachrymal and maxilla, and on its inner surface with the transverse bone. Behind the orbit it has a suture with the quadratojugal, squamosal, and postorbital.

The quadratojugal (Qu.J.) is a small bone on the side of the skull; its end covers the outer border of the quadrate, from which it is not separated by a foramen quadrati. Above it touches the squamosal and in front the jugal.

Text-figure 7.



Pnigalion oweni. Type-skull, posterior aspect, × $\frac{1}{6}$.
Reference-letters as before.

The quadrate (Qu.) is a large bone whose lower border forms the double condyle for the lower jaw; above this it rises in the skull with its outer edge connected with the quadratojugal and squamosal. The upper end of the bone and some of its hinder surface is overlapped by the squamosal.

Passing inwards from the body of the bone is a powerful pterygoid ramus, which overlaps from the squamosal on to the front face of the paroccipital process. Much of the rest of the posterior face of this ramus is overlapped by the pterygoid. Some distance above the condyle, where the pterygoid ramus joins the body of the quadrate, there is a step which may (R. 3596) be for the outer end of the extremely massive stapes.

The posterior end of the pterygoid is lightly applied to and probably usually fused with the lower end of the basisphenoid at the side of the parasphenoid. From the side of the bone in this region (49385) a small process is given off which curves round so as to shield the front of the fenestra ovalis. From this process a slender rod rises very high in the skull with its posterior edge nearly in contact with the front of the prootic: although not separated by visible suture it is probable that this bone is the epipterygoid. In R. 3594 there is a small fragment in contact with the parietal in the region of the hinder end of the ethmoid which may be the upper end of this bone.

From its articulation with the basiphenoid the pterygoid passes forwards and outwards; the outer wing is the quadrate ramus, which on account of the remarkable form of the skull and the forward throw of the quadrate, forms a nearly flat, horizontally placed sheet of bone overlapping the posterior surface of the quadrate. In front of this the pterygoid narrows and then rather suddenly widens and passes outwards to the transverse bone. Much of the anterior border is in contact with the palatine in a straight suture, but there is in 49385 a small medial process which extends forwards to touch the prevomer.

The dorsal surface of the anterior part of the pterygoid is produced into a high flange rising in contact with its fellow (with which it may be fused, 49385) as a median septum in the facial part of the skull.

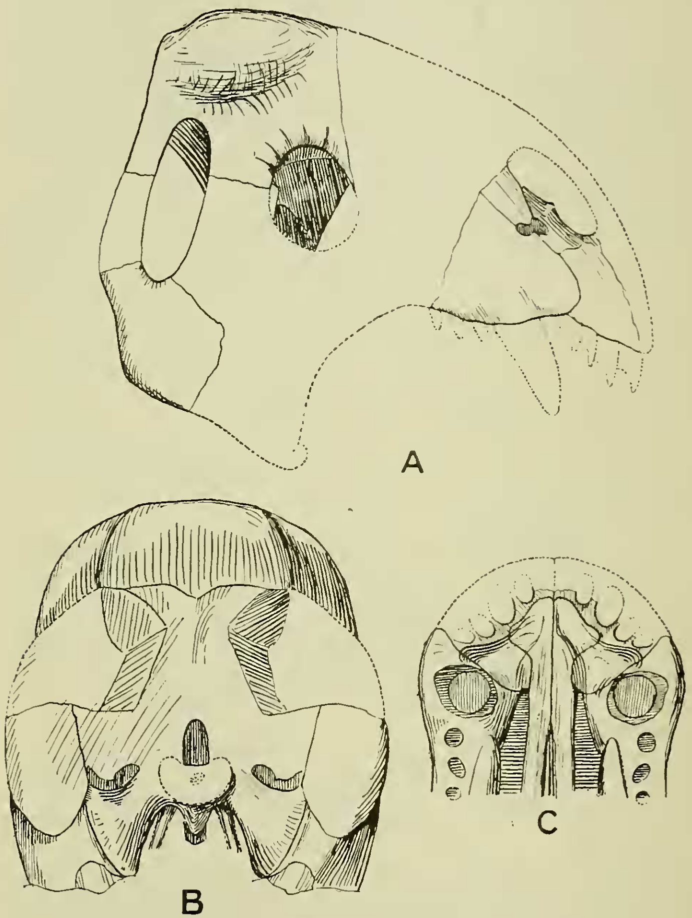
The transverse bone (Tr.) is separated from the pterygoid by incomplete but quite definite and certain sutures on both sides of R. 3594. It unites with the pterygoid to form a low flange against the side of the lower jaw, and runs outwards, having a long suture with the palatine in front to the maxilla and jugal. Where the maxilla, palatine, and transverse meet there is apparently a very small suborbital fossa only about ·5 cm. in diameter.

The palatine (Pal.) is a bone of medium size which has a suture with the transverse and pterygoid posteriorly, with the pterygoid and prevomer medially; its anterior border forms a good deal of the posterior naris and its outer edge has a long suture with the maxilla.

The prevomer (Pr.V.) is a rather remarkable bone. Behind it has a suture with the palatine, for some distance its medial surface is separated from that of its fellow by the thin vertical plate made by the pterygoids. Further forward the two bones meet in the middle line, and from this point forwards their upper surface is to a variable extent overlapped by special processes of the premaxillæ. The outer edge of the prevomer forms the whole of the inner margin of the posterior naris. From the upper margin of the bone a thin flange rises which leans inwards till its upper edge touches that of the septum formed by the pterygoids. This flange gradually declines in height, but in R. 3594 separates the subnarial process of the premaxillæ for some distance.

In 49385 the prevomer underlies the premaxillæ to the posterior edge of the alveoli.

Text-figure 8.



Lamiasaurus newtoni, gen. et sp. n.

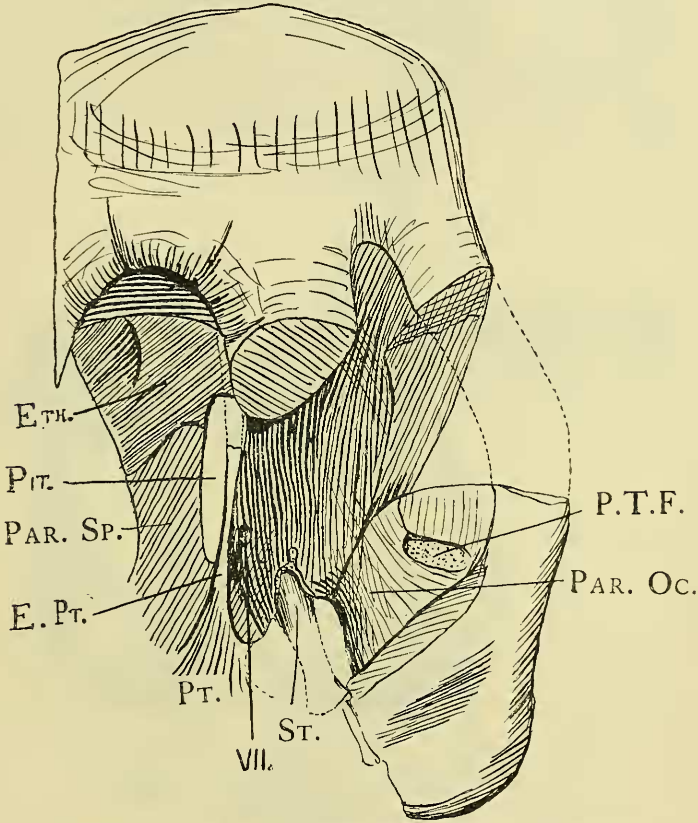
A. Right lateral aspect of the type-skull, $\times \frac{1}{6}$. B.M.N.H. 49385. There is no evidence of the relative position of the back of the skull and the snout.

B. Posterior aspect of the type-skull, $\times \frac{1}{6}$.

C. Anterior part of the palate of the type-skull, $\times \frac{1}{6}$.

The stapes (St.) in all Deinocephalia is a massive rod with few features; in 49385 it apparently fuses with the posterior lip of the fenestra ovalis. In R. 3596 it is of extraordinary size; the distal end, which is directly and powerfully articulated with the quadrate, being nearly 5 centimetres wide and 2 thick. It is not perforated for a stapedial artery.

Text-figure 9.



Type-skull of *Lamiasaurus newtoni*, external aspect of the bones of the brain-case.

Reference-letters as before, with :—Eth., Ethmoid; E.Pt., Epipterygoid; Par.Sp., Parasphenoid; Pit., Pituitary fossa; VII., 1-foramen fallopii.

The Tapinocephaloid lower jaw is represented in the British Museum only by the two dentaries of R. 3596 (text-fig. 16, A); as Dr. Broom has recently published an account of the jaw this lack is of little importance.

The post-cranial skeleton of Tapinocephaloids is represented by the following material:—

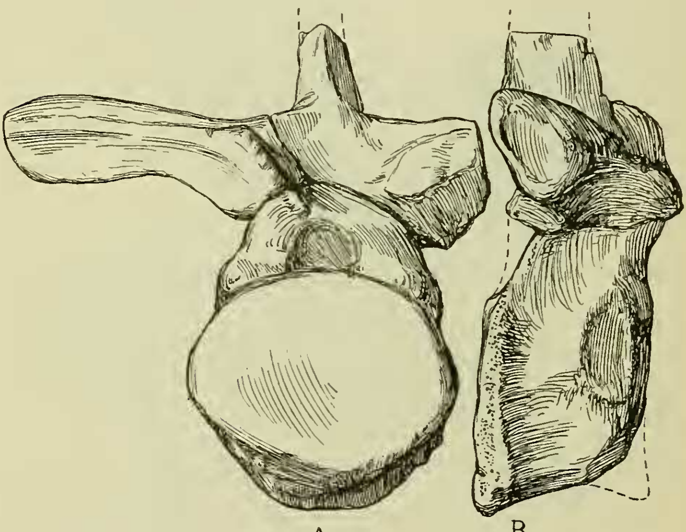
The type of *Tapinocephalus atherstonei*:—The matrix of this specimen is a dark blue grey limestone full of small lamellibranchs; these are the only bones in the collection in such a matrix.

The fragmentary skull, two nearly complete and several other dorsal vertebræ, and some caudals.

The type of *Phocosaurus* Seeley:—A sacrum and ten imperfect dorsal vertebræ. The two ilia and pubes, one ischium, two imperfect femora, a tibia, two fragmentary scapulæ, and precoracoids, one coracoid, two humeri, and one ulna.

The only fragment of skull associated with this is a bit of palate showing part of the two pterygoids and a part of the palatine. This agrees exactly with R. 3594, but is about half as large again.

Text-figure 10.



A dorsal vertebra of the type-specimen of *Tapinocephalus atherstonei* Owen, $\times \frac{1}{3}$.

A. Anterior aspect. | **B.** Lateral aspect.

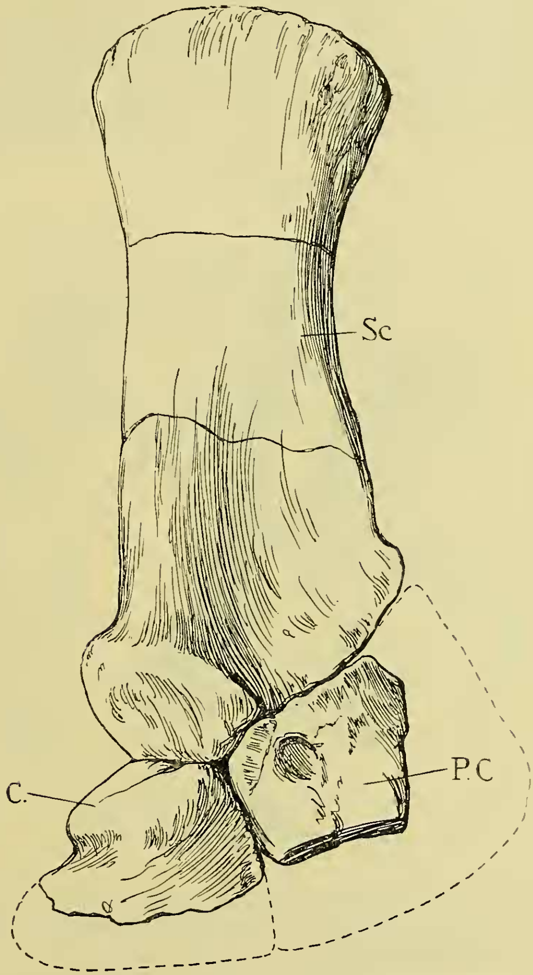
R. 1706 B.M.N.H.

Associated with the skull R. 3596 are several dorsal centra and one arch, three femora, all extremely similar, a tibia, and a humerus and atlantal intercentrum.

The atlas and axis of *Moschops capensis* have been described and figured by Broom, Bull. American Mus. Nat. Hist. vol. xxxiii. p. 139, fig. 5.

The anterior vertebræ are not well represented in the Museum collection, but have short deeply concave centra and massive arches with short transverse processes; the articular facet for the rib seems to be continuous and to be carried on the arch and

Text-figure 11.



Right scapula, coracoid and precoracoid of the type-specimen of *Phocosaurus megischion* Seeley, × $\frac{1}{3}$.

The part of the scapula between the lines which cross it is restored. It is known from the evidence of other specimens that the length is approximately correct.

C., Coracoid; P.C., Precoracoid; Sc., Scapula.

centrum equally (text-fig. 10). The later dorsals have centra like those of the anterior vertebræ, but the rib-facet is high up and near the front border. The arches are high and massive and carry long transverse processes directed nearly horizontally. The zygapophysial articulations are flat and inclined to one another and the spines not very high.

The sacrum of *Phocosaurus* is composed of four vertebræ whose centra are fused. The sacral ribs are articulated with both centrum and arch; those of the anterior two vertebræ are very massive and of about the same size, the other two are much smaller. One interesting feature is that the distal ends of the anterior sacral ribs meet and fuse before they reach the ilium.

Text-figure 12.

Right humerus of the type of *Pnigalion oweni*, × $\frac{1}{3}$.

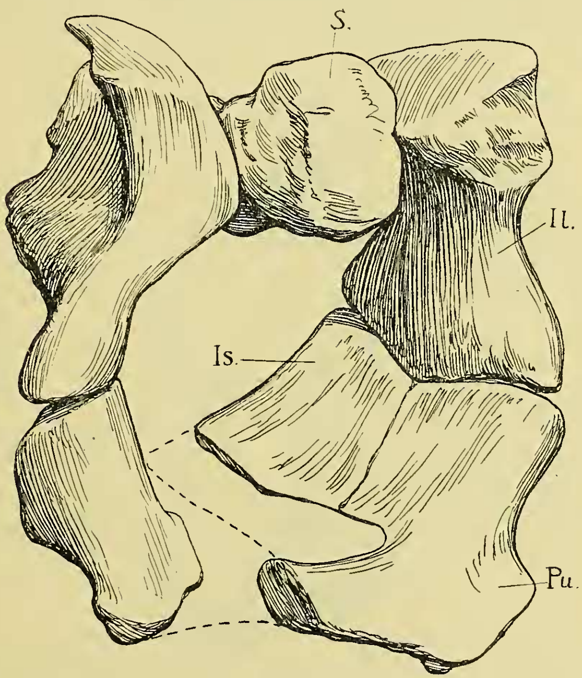
The caudal vertebræ are very short, and the series belonging to the type of *Tapinocephalus* seems to taper rapidly, so that the tail was undoubtedly short.

The shoulder-girdle of Tapinocephaloids seems to be very large and massive in comparison with the skull.

The scapula (Sc., text-fig. 11) is represented by its well-preserved lower and upper ends in *Phocosaurus* and by an isolated bone which gives the length. It has a flat blade with no indication of an acromial process. The lower end has a long, straight face for articulation with the precoracoid. Behind this it thickens and forms the upper part of a glenoid cavity which looks outwards and slightly backwards.

The precoracoid (P.C., text-fig. 11) is a very large bone articulating by a long suture with the scapula and bearing a long articular face for the coracoid. It is pierced by a foramen which opens into a distinct pit on the visceral surface. The coracoid (C., text-fig. 11) is a large bone which has a long surface for contact with the precoracoid, and whose upper anterior corner articulates with the scapula. Behind this contact it forms the lower portion of the glenoid cavity, which is entirely formed by the scapula and coracoid.

Text-figure 13.



Sacrum and pelvis of the type-specimen of *Phocosaurus megischion* Seeley; seen obliquely from front. $\frac{1}{6}$ nat. size.

Il., Ilium; Is., Ischium; Pu., Pubis; S., Sacrum.

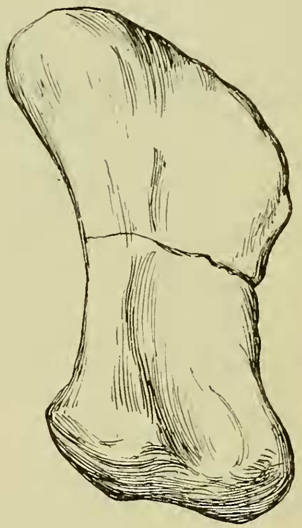
The humerus (text-fig. 12) is a very massive bone with expanded ends which are in planes at a considerable angle to one another. The head is cylindrical and directly continuous with the enormous deltoid crest, which, after extending more than halfway to the distal end of the bone, suddenly subsides into the shaft. The shaft is relatively slender but very short, and soon expands into the broad distal end. This is furnished with two articulating faces: one almost entirely represented by a low knob on the anterior face of the bone for the radius, the other on the end for the sigmoidal fossa of the ulna. There is a large entepicondyle, and a foramen piercing the shaft just at the end of the deltoid crest.

The ulna is a short massive bone, with a pronounced olecranon process and a facet for the head of the radius.

The pelvis of *Phocosaurus* (text-fig. 13) has already been described by Seeley, and its general character will be best understood from the figures of this paper. The interesting features are the small pubic foramen, the absence of any obturator foramen, and the enormous size of the acetabulum.

The four sacral ribs articulate with the inner surface by large facets, which are continuous with one another.

Text-figure 14.



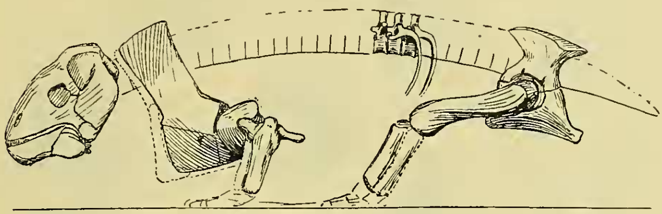
Left femur of the type of *Pnigalion oweni*, × ⅓. R. 3596.

The femur (text-fig. 14) is a very large bone with a rounded head and long and large external trochanteric ridge, which slowly subsides on to the shaft. The lower end is provided with two condyles, which are only obscurely separated from one another. The bone as a whole is flattened dorso-ventrally.

The tibia is a bone with very few features; it has an expanded head and a short, thick shaft.

The restoration of the skeleton (text-fig. 15) founded on all this material gives one an idea, which is probably generally correct, of the habit of the group. The striking features are the small head and very massive limb-girdles. *Phocosaurus* is relatively more heavily built than "*Pariasaurus*" *baini*.

Text-figure 15.



Restoration of the skeleton of a Tapinocephaloid.

Skull, humerus, femur, and tibia from the type of *Pnigalion oweni*; other bones from the type of *Phocosaurus*.

Dentition and Systematics of Tapinocephaloids.

The type-specimen of *Tapinocephalus atherstonei* has been ground down so as to show many sections of uncut tooth-crowns and of the roots of functional teeth. Judging from these the teeth are similar all round the upper jaw, there being no enlarged canine.

The teeth-crowns, as shown by the series of sections which cut them at many levels, consist of a sharp upstanding cusp, the outer side of which is rounded and the inner side flattened; from the lower border of this cusp the crown is continued inwards on a large shallowly concave area surrounded by ridges descending from the sides of the anterior cusp; these seem to be smooth, and the outer is the larger. An isolated tooth (text-fig. 16, B) in the Museum collection seems to agree with the tooth-crown restored from the sections shown in this type-specimen.

R. 3594, which may be called

Mormosaurus seeleyi, gen. et. sp. n. (Pl. IV.),

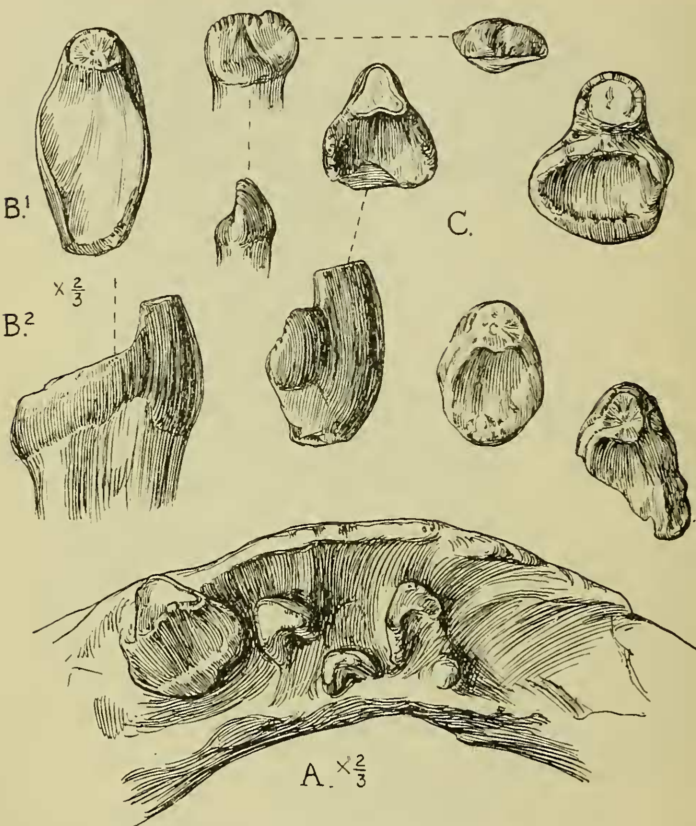
has an extremely feeble dentition, which is quite uniform throughout so far as can be judged from the usually imperfect crowns and alveoli. Each tooth seems to consist solely of a cusp which is oval in section and has a coarsely serrated edge.

R. 3596 may be called

Pnigalion oweni, gen. et sp. n.

The dentition of the upper jaw is not known, but there is no sign of an enlarged canine in the dentary. The teeth seem to be similar all round the mouth. Each tooth consists of a high outer cusp with a rounded external surface and a deep groove down its inner side. All round the inner side and front and back of this cusp rises a strong cingulum, whose margin is raised and serrated so as to form a cup in the middle of the crown.

Text-figure 16.



Deinocephalian teeth.

A. Right dentary of type-specimen of *Pnigalion oweni*, × $\frac{2}{3}$.
B. *Tapinocephalus*?, × $\frac{2}{3}$.
C. Series of teeth of one individual of unknown genus, × 1.

No. 49385 may be called

Lamiasaurus newtoni, gen. et sp. n.

The dentition of the upper jaw consists of four large incisors represented only by their alveoli, which are oval in shape and suggest that the teeth may have been like those of *Deuterosaurus*.

There is a single canine, which is large, strongly inclined forwards, and circular in section. Behind this there are three molars, shown in transverse section to be circular and relatively small; it is probable that there was one more only.

One important difference between this type and the preceding three is that whilst they all have very numerous replacing teeth, which are not in the same stage and were thrust up indefinitely like those of a crocodile, in *Lamiasaurus* there is no trace of successional teeth.

The other types of South African Tapinocephaloids which have been described are:—

Delphinognathus conocephalus, a much smaller form without large canines, of which the details of the dentition are not known.

Moschops capensis, also a small form with no canines and with no details of the dentition.

Taurops macrodon, a large form apparently with teeth somewhat like those of *Tapinocephalus*, but not sufficiently described or figured to be definitely identified at present.

Eccasaurus priscus, founded on a humerus of rather unusual type, to which is referred a tooth of the general plan of *Tapinocephalus* but of a narrower oval form and more cuspidate.

Moschognathus whaitsi, founded on a figured lower jaw which, as it seems to contain no teeth, is indeterminable.

The Titanosuchid branch of the Deinocephalia is represented by the following skull-material in the British Museum (Natural History):—

An imperfect skull (Pl. V., & text-figs. 17, 18) consisting of the dorsal surface from behind the nostrils to the back, with the squamosals and part of the zygomatic arch; and a block which has a rather poor fit with the upper part, but contains a good deal of the maxilla and prevomers and a small fragment of the palatine.

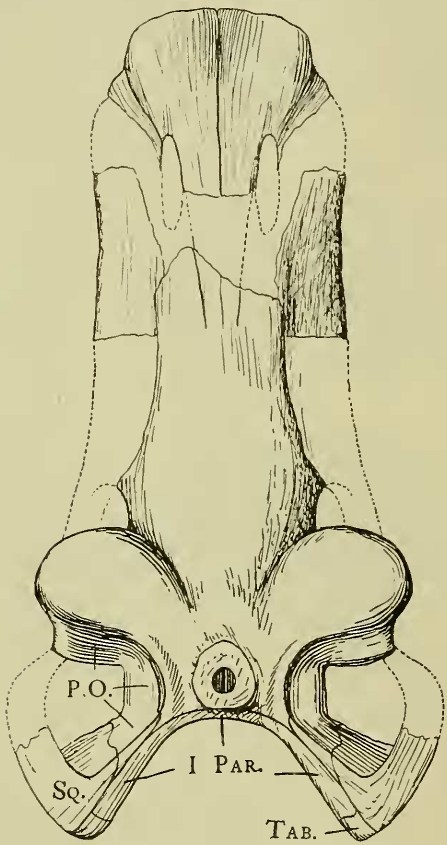
This specimen (R. 3595) was collected by Prof. Seeley at Tamboer Fontein. The only other skull-materials I have used are the premaxillæ of the type-specimen (49370), which itself consists of the associated remains of two individuals of identically the same size. The maxillæ of these agree exactly, so far as can be seen, with that of the specimen mentioned above.

Nothing is known of the basicranial part of the skull, but the supraoccipital above the post-temporal fossæ is present in the Tamboer specimen. It is a flat wide plate with rather large post-temporal fossæ bounding it below, and the upper part of the deep and narrow brain-cavity impressed on its lower surface. Its posterior surface is overlapped by the interparietal and tabulares, and its upper edge is in contact and perhaps fused with the parietals.

A small part of the ethmoid remains in contact with the under surface of the frontals, and is a small bone with a very small cavity for the olfactory lobes of the brain.

The interparietal (I. Par., text-fig. 17) is a very large vertically placed plate on the back of the skull. Its anterior face is in contact with the upper part of the supraoccipital and the posterior ends of the parietals. Laterally it overlaps the parietal rami of the postorbital and squamosal and the tabulare.

Text-figure 17.

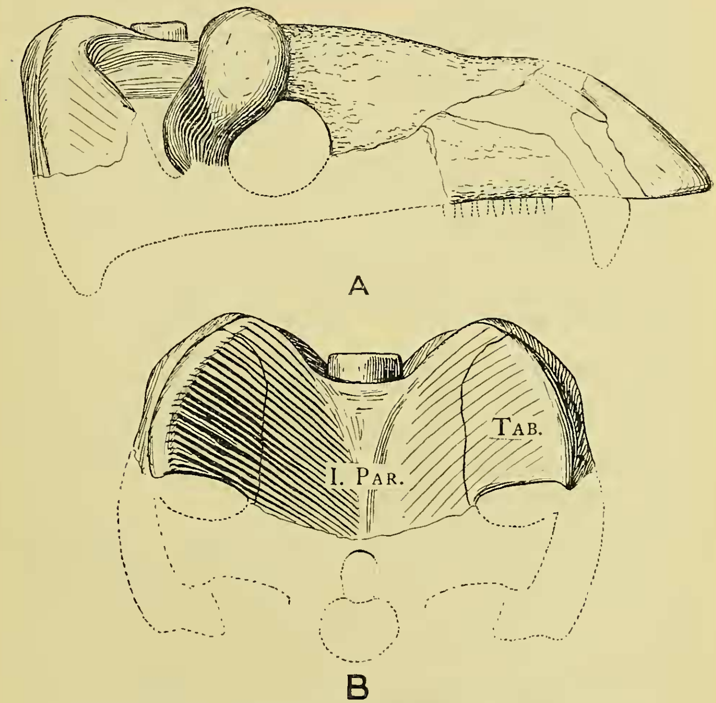


Titanosuchus. Dorsal aspect of skull. Premaxillæ from type.
The remainder from R. 3595 B.M.N.H. × ⅙.
P.O., Postorbital; Sq., Squamosal; I.Par., Interparietal; Tab., Tabulare.

The tabulare (Tab., text-figs. 17 & 18 B) is a large bone, whose medial border is covered by the interparietal and whose anterior face has a contact with the supraoccipital, postorbital, and squamosal. Its lower border forms the upper side of the post-temporal fossa, and its outer edge is thickened and with the squamosal forms a long, vertically placed auditory groove.

The squamosal (Sq., text-fig. 17) is only incompletely preserved; as shown it has a parietal ramus, which covers much of the front face of the tabulare and extends inwards to overlap the posterior end of the postorbital. With the tabulare it forms the auditory groove on the postero-lateral corner of the skull, and beyond this sends forwards a massive zygomatic part on the outer surface of the skull.

Text-figure 18.



A. *Titanosuchus.* Lateral aspect of the same specimen as text-fig. 17.

B. *Titanosuchus.* Posterior aspect of skull. B.M.N.H. × $\frac{1}{6}$.

I.Par., Interparietal; Tab., Tabulare.

Except for the suture with its fellow and the frontal, the parietal is completely shown. It is a small bone in contact with its fellow except for the pineal foramen, which is a round hole. The two bones form a special little projection raising the opening more than a centimetre above the general line of the surrounding bone.

The sutures surrounding the postorbital (P.O.) are all visible, but that with the postfrontal only on the ventral surface. The bone forms a massive sheet at the back of the orbit, and forms the hinder part of the extraordinary mass of bone which overhangs it; it sends back a powerful process along the side of the parietal, which forms the inner border of the temporal fossa, and thence runs outwards along the front face of the tabulare to be covered by the squamosal.

The sutures separating the postfrontal from the postorbital and prefrontal are only visible on the under surface: they are straight and run inwards for a very long distance with the postfrontal as a narrow strip between them. It probably forms a good deal of the knob above the orbit.

The sutures between the prefrontal and lachrymal etc. are not visible, but on the under surface it seems that the nasals are narrow bones, each carrying a sharp-edged rib, so as to form a groove on the lower surface.

At the anterior end the specimen shows on the outer surface traces of the sutures between the internarial processes of the premaxillæ and the nasals. It is evident that they were very long.

The premaxillæ known from the type-specimen have a flat facial surface and rather broad internarial processes, the nares being on the dorsal surface some distance behind the snout.

The palatal surface of the premaxilla is entirely formed by its tooth-bearing edge, and the lateral border is in contact with the maxilla.

The maxilla is a large bone with a great facial expansion. Its palatal exposure is solely formed by its dentigerous margin, and it is in contact with the palatine. There are large prevomers with a long interchoanal bar, the dorsal surface of which rises into a high thin flange. Of the quadrate only the articular edge is known, which gives no indication of its size.

The type-specimen of *Titanosuchus ferox* gives many bones of the lower jaw, all disarticulated. The articular is a small bone with a cotylus for the quadrate condyle, which apparently faces very nearly backwards. The postarticular part is only represented by a small process on the lower side of the bone. The anterior part rapidly narrows and finishes in a point. There are well-marked articulating surfaces for the prearticular and surangular. The angular is flat, and has a deep and very narrow notch covered with a reflected lamina exactly as in a Gorgonopsid. The dentary is a very massive bone, with a deep groove on its inner surface for the prearticular, surangular, and angular The bone seems to give evidence that there was no freely projecting coronoid process. One interesting feature is that there is a very shallow, but quite definite, step in the dentigerous margin behind the canine, as in Gorgonopsids, but, of course, relatively very much smaller.

The lower surface of the dentary has a broad surface for the splenial, which must have formed the whole of the lower border of the anterior part of the jaw, and had a large symphysis with its fellow.

The post-cranial skeleton of Titanosuchids is represented by two series of bones:—

The type-specimen of *Titanosuchus ferox* (two individuals): neural arch and intercentrum of atlas, vertebræ, scapulæ, coracoid, cleithra, clavicle, three humeri, femur, and fibula.

A series of associated bones of another genus, comprising vertebræ, ribs, ilium, humerus, femora, tibia, and skull-fragments.

The atlantal neural arch is absolutely identical with that of the Dicynodont *Kannemeyeria*, as is the intercentrum. They give evidence that the whole complex was similar to that of *Moschops*, as described by Broom.

The vertebræ of *Titanosuchus* are all extremely unsatisfactory, but seem to be generally similar to those of Tapinocephaloids, with longer neural spines and shorter transverse processes; it is just possible that the capitulum and tuberculum were connected by a very thin web.

The other specimen has very high neural spines.

Certain fragments of bone belonging to the type of *Titanosuchus* suggest the presence of relatively feeble abdominal ribs.

The scapulæ are very much weathered, but are extremely large and massive bones, giving no evidence of an acromion.

The coracoid is essentially identical with that of the Tapinocephaloids, and shows clearly that the precoracoid was excluded from the glenoid cavity.

The cleithrum is a fine bone, nearly 8 centimetres wide and 2 thick; it has an articular facet for the front edge of the scapula.

What is almost certainly the lower end of the clavicle is represented by an unsymmetrical sheet of bone about 20 cm. by 30 cm., which has the root of a powerful process arising from one surface just within the edge. There is no other bone in the skeleton it can possibly be, and, if it is correctly determined, the interclavicle must have been an extraordinary wide flat sheet.

The humerus as figured by Seeley, Phil. Trans. 180 B, pl. xx. figs. 1 & 2, gives a rather misleading idea of the bone. It is in essentials much like that of the Tapinocephaloids, but differs in its relatively narrower lower end, in having the facet for the head of the radius still more on the front of the bone, and the two openings of the entepicondylar foramen on the same side of the shaft. Finally, there is a small ectepicondylar foramen.

A single ulnare is present in the material; it is a rather small but thick bone with a notch in one border, forming part of the ordinary foramen between the ulnare and the intermedium.

The ilium is very incomplete, but is a short bone, apparently similar to that of the Tapinocephaloids.

The femur differs from that of the Tapinocephaloids in its relative slenderness and the lesser size of the trochanter.

The tibia does not differ essentially from that of Tapinocephaloids.

General Discussion.

That the animals whose structure I have discussed under the heading of Tapinocephaloids are all closely allied admits of no discussion, and is self-evident in every detail of their structure.

To the same group belongs the Russian type *Deuterosaurus*. As shown clearly by Eichwald's figures, the dentition is absolutely characteristic, the powerful incisors which interlock are structurally identical with those of *Tapinocephalus*. The enlarged canine so clearly shown in his figures occurs in the remarkable type *Lamiasaurus* which I have described above, and the presence of only a single molar is a variation of slight importance. The skull figured by Prof. Seeley has all the characteristic features of the group, the broad zygomatic arch with the postorbital obviously widely meeting the squamosal and the covering of the side of the parietal by the postorbital (as shown and lettered "post-frontal" in Seeley's figure) being identical with the structures in the South African forms. Even the slight difference in the narrowness of the intertemporal bar and the crest on the parietals can be matched in a fragment from South Africa in the British Museum. Seeley's figure also seems to show that there was the very characteristic vertical area of basioccipital below the condyle and the large quadrate characteristic of the group.

The Russian type *Rhophalodon* and that described by Twelvetrees as *Cliorhizodon orenbergensis* (R. 4077), which is perhaps generically identical with the previously described *Deinosaurus*, are apparently closely allied to *Titanosuchus*. *Cliorhizodon* (at any rate, as shown by the beautifully preserved type-specimen in the British Museum) is extraordinarily like a small *Titanosuchus*, as was, in fact, recognised in the original description. There is nothing in the whole structure of the skull to prohibit a connection.

Whether *Titanosuchus* is really closely allied to the Tapinocephaloids, or whether it is a specialised Gorgonopsid, as Broom now believes, is perhaps more doubtful. It resembles the Tapinocephaloids in the extraordinary thickening of its skull and in the whole texture of all the bones.

The whole structure of the temporal region, the form of the squamosal, and the relations of the tabulares (postorbitals, parietals, and squamosals) are identical in the two types. The very curious auditory groove is the same in each type. The premaxillæ of *Titanosuchus* have a thoroughly Tapinocephaloid appearance, and the position of the external nares far behind the end of the snout on the dorsal surface is unparalleled in Therapsids, except in that group.

If *Rhophalodon* is indeed related to *Titanosuchus*, then in the large quadrate and the vertical area of basioccipital below the condyle we have very striking resemblances to the contemporary Tapinocephaloids.

Finally, so much of the palate of *Titanosuchus* as is known is quite unlike that of any Gorgonopsid, whilst it strikingly resembles in detail that of *Lamiasaurus.* We are, I think, therefore justified in regarding the two as divergent branches of the great order Deinocephalia.

That the Deinocephalia are Therapsids has never been questioned of recent years. The whole character of the limb-bones, particularly the humerus, is quite like that of the corresponding parts of an Anomodont, and is unknown in any other group. The shoulder-girdle with the precoracoid excluded from the glenoid cavity is extremely like that of a Gorgonopsid, and, except for its lack of an acromion, that of *Dicynodon.* No similar arrangement is known in any other group of reptiles. In the more fundamental features of its skull-structure, the wide occipital plate with the small and greatly separated post-temporal fossæ, the high brain-cavity, and the low position of the vestibule of the ear, it agrees exactly with all South African Therapsids. As is shown clearly by Dr. Broom's figures of the lower jaw and by that of *Titanosuchus,* it has the characteristic flat angular and notch of the Therapsids.

The group has, however, a very special importance, because alone amongst the South African forms it retains a large quadrate. The Tapinocephaloid quadrate is relatively as large as in any other reptile—as large, for instance, as that of a Tortoise. The importance of this is that it shows that the reduction of the quadrate, which is so noticeable a feature of the Anomodonts and "Carnivorous" Therapsids, is not an essential feature of Therapsid structure, but has developed in comparatively late times in at least two branches independently (I intend to adduce evidence in support of this statement in a later paper). Some years ago, in describing the skull of *Diademodon,* I pointed out that this reduction of the quadrate was part and parcel of a whole series of changes which led to the reduction of all regions of the skull (the basisphenoidal, basioccipital, and exoccipital regions in particular) which lay below the base of the brain. This generalisation is justified by all subsequent work on Therapsids, and is well illustrated by the great depth of the basicranium in Deinocephalia, an arrangement which may to some extent be paralleled in Deinosaurs.

The exact relation of the Deinocephalia to other South African groups of Therapsids is not easily determined.

The skull of *Titanosuchus* bears a very considerable resemblance to that of a Gorgonopsid, modified, of course, by its great thickness and the large bony bosses over the orbits. It is distinctly more primitive in many features—for instance, in the less widely spread zygomatic arches. The skulls of the more primitive Gorgonopsids, however, show no trace of the vertical area of basioccipital below the condyle; and there are no features of the auditory region of the brain-case which in any degree suggest that they have been derived from a type with a Deinocephalian structure. It will be remembered that *Rhophalodon*, which is in many ways extremely like a Gorgonopsid, has this characteristic Deinocephalian structure. So far as the lower jaw goes, the Gorgonopsids could be derived directly from a lightly built Titanosuchid. The post-cranial skeleton, so far as is known, is also very similar, allowing for the differences due to the great weight of all well-known Deinocephalians or, using as a term of comparison, the relatively slender bones from the Ural copper-mines.

In fact, it is legitimate to assume that Deinocephalia and the Gorgonopsids arose from a not very distant common ancestor, but that they subsequently pursued quite different paths.

Perhaps the most interesting comparison is with the Anomodonts. In many features (the upturned parasphenoid and the structure of the ethmoid, for example) there is a distinct resemblance between the two groups, which also resemble one another to some extent in the shortness of the brain-cavity—in some types, at any rate. Further, many Anomodonts have a considerable vertically placed area of bone below the basioccipital condyle, which may be compared with that in Tapinocephaloids. As this area does not exist in *Endothiodon*, whilst it is most pronounced in *Lystrosaurus*, it is probably a secondary specialisation independently acquired within the group. Connected with this feature, however, is the development of that curious process of the vestibule which carries the fenestra ovalis down to the lower border of the skull. This curious detail is found even in *Endothiodon*, a rather primitive type, and is apparently quite a fundamental character of the group.

Although the cavity of the inner ear has not been cleared in any Deinocephalian, there can be no doubt that a similar structure did occur in that group—a fact which suggests a nearer relationship between the two groups than either of them hold with the Gorgonopsid line.

At the same time the Deinocephalia differ from all other South African Therapsids in the mode of articulation of the ribs in the dorsal region.

The most interesting comparison is between the Deinocephalia and the Pelycosauria, using that term to cover all the "Texas" Therapsids.

If we compare a Deinocephalian with the very primitive *Varanosaurus*, we find many resemblances. We have, to begin with, the characteristic Therapsid characters of the occiput and lower jaw. In addition, we find that there are striking resemblances between the quadrates of the two types in their size, relation to the squamosal and quadratojugal, and in the powerful step for the distal end of the stapes. Another resemblance is in the form of the squamosal, which in both types is a simple sheet folded round the back of the quadrate, and not produced outwards as in the Anomodonts and Therocephalia. The occurrence of a vestigial "supratemporal" in *Varanosaurus* is a primitive feature of little importance.

Comparison of a Tapinocephaloid with *Dimetrodon* leads to some interesting results, as Broom has already pointed out. There is a resemblance in shape, owing to the very short temporal regions and high and compressed form of the skull in both groups. The basicranial region of *Dimetrodon*, although more specialised than that of *Varanosaurus*, shows no suggestions of the characteristic Deinocephalian structure, and is, in fact, extremely like that of the more primitive of the Gorgonopsids. The very peculiar parasphenoid is identical in the Deinocephalia and *Dimetrodon*, and it is probable that the ethmoids are also similar. The quadrate of *Dimetrodon* is modified from its primitive condition by that development backwards of the posterior angles of the skull which is shown by the curious backwardly directed processes of the outer ends of the paroccipital processes. Making allowance for this modification, its relations to the surrounding bones are essentially those held by the corresponding bone of *Mormosaurus*, so far, at any rate, as can be judged from published descriptions. In the palate also there are distinct resemblances in the development of the high vertical flanges from the pterygoids and prevomers. The two types are, however, specialised in directly opposite directions, one with a short face for a herbivorous diet, the other with the elongated gape which is necessary to a carnivorous animal with the characteristic reptilian habit of grasping its prey after a single snap.

The occiput of *Edaphosaurus*, as figured by Williston and Case, is extremely like that of *Pnigalion*, and, if we may judge by *Varanosaurus*, was essentially similar in structure.

Finally, as Broom has pointed out, the face of *Dimetrodon* is structurally very similar to that of such a Deinocephalian as *Mormosaurus*—it is perhaps even more similar to that of *Deuterosaurus*.

On the whole, the Deinocephalian skull resembles that of the Pelycosaur more closely than it does any other South African Therapsid.

As Broom has already shown, the lower jaw of a Tapinocephaloid, except for the differences due to the oppositely specialised dentitions, is structurally very similar to that of *Dimetrodon*. It differs, however, in the more greatly developed Therapsid notch.

Broom has already shown the very striking resemblance between the Pelycosaur vertebræ (particularly those of *Dimetrodon*) and those of Tapinocephaloids.

In the rest of the post-cranial skeleton, however, there is very much more similarity between the Tapinocephaloids and the other South African Therapsids than between that group and the earlier Pelycosaurs.

In the cartilaginous shoulder-girdle the precoracoid is entirely excluded from the glenoid cavity, and there is no trace of the screw-shaped form of the articular surface which is an essential feature of the primitive type. The humerus also is of a more modernised form, its action being an up and down movement instead of one which is nearly parallel to the ground. The very broad lower end of the clavicle of *Titanosuchus* is, however, a point of resemblance with the earlier forms.

In the pelvic limb we find a somewhat similar mixture of characters.

The whole pelvis, for example, is somewhat similar to that of *Dimetrodon*, particularly in the production of the outer corner of the front border of the pubis and its deflection, more so perhaps than to any South African type; but the femur is of a modernised type strongly resembling that of *Dicynodon*.

The final result is that the presence of the Deinocephalia makes it impossible to exclude the American Lower Permian and Carboniferous Pelycosaurs from the later South African Therapsids. Such a division could at any time have been drawn only on the more primitive limbs and large quadrate of the early forms; the fact that in Deinocephalia we have types with a quadrate as large as that of the Pelycosauria combined with modernised limbs renders the foundation of a great group-division on these characters quite impossible.

For this great stem of the Reptilia, including all the mammal-like reptiles, many names are available. I am myself inclined to extend Broom's Therapsida, a most appropriate name, to the whole of them, but I fully recognise that Cope's earlier names of Theromorpha and Theromora have been used in the same sense; these names were never very clearly defined by Cope, and have at one time or another included nearly all Permian reptiles. If anyone should wish to resuscitate these names in this connection, I would point out to them that Owen's term Anomodontia was used by that author in 1860 in a wide sense to include the Dicynodonts and also carnivorous Therapsids from South Africa, and has at least as good a claim to be used as Cope's later terms.

Discussion of Special Features of the Skull.

The septomaxilla of Deinocephalia is of interest on account of its variability. It resembles that of all other Therapsids, except certain Cynodonts and Anomodonts, in the fact that there is a foramen behind it opening from the outer surface into the nasal cavity. It is of interest that this foramen was first described by Case in *Dimetrodon*. It is evident in the majority of the more primitive South African "Carnivorous" Therapsids, and is clearly shown in a British Museum skull of *Endothiodon* and in Prof. Sollas's model of *Dicynodon*. Its function is unknown, the only suggestion I have yet found is that it may mean that the ductus naso-lachrymalis opened on the surface; it will be remembered that in the small Temnospondylous Stegocephalian

Micropholis this duct runs forwards completely in the lachrymal bone to the posterior end of the septomaxilla, and it appears from its mode of development to have been primitively a mere surface-groove.

The squamosal of Deinocephalia is of some interest; in its relations to all other bones, particularly those of the otic capsule, the quadrate, tabulare, postorbital, and parietal, it agrees exactly with the corresponding bone of the more primitive Gorgonopsids, which is clearly identical with the squamosal of *Diademodon*, which is clearly homologous with the bone of the same name in Mammals. The squamosal of a Deinocephalian is clearly the same as the large temporal element in *Varanosaurus*, having similar relations to the paroccipital, postorbital and tabulare, and only differing in retaining its primitive connection with the pterygoid. As this type retains a small "supratemporal," there is now no doubt that the squamosal is the outer of the three temporal bones in primitive Reptilia.

The Auditory Arrangements of the Therapsids.

Of recent years belief in the truth of Reichert's hypothesis of the homologies of the mammalian ossicula auditus has been gradually growing, and the fine work of Gaupp has practically placed it beyond question. At the same time, Broom, following a suggestion of Seeley's, has shown how in the gradual increase in size in the dentary and the decrease of the other elements of the jaw and the quadrate, the "carnivorous" Therapsids gradually approach the mammalian condition. The same author has pointed out that the stapes is articulated with the quadrate in Therapsids just as is the stapes of mammals with the incus. Finally, following on my own more accurate account of the Therapsid jaw, Mr. Palmer has shown the extraordinary similarity in detail between the lower jaw (including the dentary, malleus, prearticular, and tympanic) of a mammary fœtus of *Perameles* and that of the advanced Cynodont *Diademodon*.

The homologies of the various bones being now placed beyond dispute by the work of these authors, it is desirable to carry the inquiry further and discuss the position and changes of the tympanic membrane and other parts of the ear.

The stapes of Therapsids is in all cases where the condition is known articulated with the quadrate. In the following types, *Cynognathus*, *Trirachodon*, *Nythosaurus*, *Arctognathus*, *Lycosaurus*, *Dicynodon*, *Lystrosaurus*, *Diælurodon*, *Kannemeyeria*, *Mormosaurus*, *Pnigalion*, *Lamiasaurus*, *Dimetrodon*, *Varanosaurus*, which cover the superorder very fairly, the stapes has actually been seen in place; the facet on the quadrate for its distal end is shown in very many more forms.

Quite recently, when discussing the primitive Therapsid *Varanosaurus*, I pointed out that in many ways it greatly recalled the

Cotylosaurian family of the Captorhinidæ, so much so that a blood-relationship between them seemed most probable.

Prof. Williston had still earlier expressed a similar opinion:—"That we have in *Labidosaurus* and its allies a persistence of those generalized characters which gave origin to the peculiar specializations of the Pelycosaurs." One of the peculiarities of these Captorhinids, in which they differ from all other known Cotylosaurs, is the fact that they have a stapes whose distal end is articulated with the quadrate. We have therefore some justification for assuming that this peculiar condition in the Therapsids has not arisen within that group, but has descended to it from its ancestors.

I have shown that there are very strong reasons for believing that the reptiles have arisen from the embolomerous Stegocephalia, which are the only group of Tetrapods known in Lower Carboniferous rocks. In figure A, in the plate of my paper on "The larger Coal-Measure Amphibia," Manchester Memoirs, vol. lvii. pt. i., there is shown a very definite depression on the upper surface of the quadrate and pterygoid. This definite pit occurs in all embolomerous Stegocephalia in which I have examined this region, and is obviously of importance. The only explanation I can find for it is that it received the outer end of the stapes. It is important to note that in the uncrushed skull it must have looked towards the auditory region. There is thus a suggestion of evidence that the Cotylosaurs of the family which gave rise to the Therapsids and the Captorhinids received the condition of having the distal end of the stapes articulated with the quadrate from their amphibian ancestors, as they in turn passed it on to their descendants.

There are strong reasons for believing that the Stegocephalia have arisen from the Rhipidistian group of the Crossopterygian fishes (the Osteolepids), which were no doubt technically, though probably only to a slight extent, functionally hyostylic. In these fishes the hyomandibular, which has been seen only by Dr. Traquair in *Rhizodopsis* (an observation I have been unable to check from the material in the British and Manchester Museums, which includes at least the greater part of that which was before Dr. Traquair), no doubt articulated with the otic region of the cranium and with the quadrate, as in all fishes. There are many reasons for believing that the stapes of a Tetrapod is homologous with the hyomandibular of a fish, and it is probable that in the embolomerous Stegocephalia, which had just arisen from fishes, the primitive connection between the distal end of the hyomandibular or stapes and the quadrate was retained. In later Amphibia (*Eryops*, *Trimerorachis*, *Cyclotosaurus*, to mention only types in which it is known in place) it lost this connection, and its distal end is connected with a tympanic membrane stretched across the otic notch.

It thus seems to be fairly probable that the connection between the distal end of the stapes and the incus in a mammal has been directly derived from the connection of the distal end of the hyomandibular and the quadrate in its far-off fish-ancestor, and that this connection has never been lost in the phylogeny of the group.

The most primitive lower jaw known amongst Therapsids, that of *Dimetrodon*, as it has been described and figured by Case, Williston, and Broom, is differentiated from that of a member of any other Reptilian superorder by the characters of its posterior part, and particularly the angular. In *Dimetrodon* the angular is essentially a flat plate whose upper border overlaps the surangular and is itself overlapped by the dentary in the usual way, whilst its lower border forms the lower border of the jaw. The posterior end of this bone is separated from the outer side of the prearticular by a notch, so that the border stands out freely. The whole jaw is very narrow from side to side, the Meckelian vacuity being reduced to a very narrow slit between the prearticular and the surangular. The flat plate-like angular and the notch in its posterior border are the characteristic features of this jaw, and are found in all Therapsids which are properly known and in no other reptiles whatsoever.

The Deinocephalian jaw only differs from that of *Dimetrodon* in the further enlargement of the notch, which in this type extends forwards so as to form a deep pocket in the substance of the angular. In such Therocephalians as *Scylacosaurus* the condition of the angular is almost exactly as in Deinocephalia, there being a deep but very narrow pocket in the substance of the angular which forms a large reflected lamina outside it. The foramen shown in the angular in many of Broom's figures of Therocephalian skulls has no existence in fact, as such, but is merely the anterior end of the notch.

In the Gorgonopsids there is the usual notch and reflected lamina, which is, however, small, never reaching the size of that of *Scylacosaurus*. This notch in the higher Gorgonopsids, *e. g.* *Arctognathus*, seems to move relatively further forward. Finally, in the Cynognathids, which have a "look" of the Gorgonopsids, of a character that cannot be intelligibly expressed in words but is very striking to anyone accustomed to handling the two types, and suggests that they are in all probability genetically related, the notch has moved still further forward, and the reflected lamina now stands downwards from the rest of the bone as a very slender process. The extraordinary resemblance of this bone to the tympanic of the pouch fœtus of *Perameles* (or of *Dasyurus*) seems to me to raise a very strong case for believing that *Cynognathus* and its allies had a tympanic membrane spread between the divergent branches of its angular. The actual shape of the bone makes such a position possible, the hinder end of the membrane being carried by the ridge on the lower side of the squamosal, which lies just outside the end of the paroccipital process, and on the musculus depressor mandibuli, if such a muscle be present. A membrane in this position stands nearly vertically in the skull, and lies at the lower and inner end of the groove which Broom and I, following the original identification of W. K. Gregory, regard as an external auditory meatus. If this position was really that held by the tympanic membrane in *Diademodon*, then in that type the tympano-tubal cavity had already grown up round the bones of the back of the lower jaw. If this position of the membrane be correct, by tracing back along the series of Gorgonopsids to the Deinocephalia, we ought to have self-consistent results throughout, and to arrive at a condition in primitive forms which is not inconsistent with that found in known Reptilia. The series of Gorgonopsids at my disposal gives a sufficiently close morphological series to show with certainty that:—

1st. The notch in the hinder border of the angular of a Deinocephalian is homologous with the wide triangular notch in *Diademodon*.

2nd. That the very small but distinct auditory groove described above in Deinocephalia is homologous with that of *Diademodon*.

3rd. That the ridge to the outer side of the paroccipital on the squamosal in the two types is the same.

These homologies lead us to expect that the tympanic membrane of Deinocephalia should be attached to the squamosal just outside the paroccipital process, to the posterior surface of the quadrate, and to the edge of the reflected lamina of the angular. I believe such an attachment to be workable inasmuch as a tympanic membrane attached to it might be flat.

The groove for the external auditory meatus in Deinocephalia is of great interest. It is undoubtedly homologous with that of *Diademodon*, and I think almost as certainly with that of a mammal. It gives clear evidence that even at this time the tympanic membrane (whatever its precise situation and attachments) had sunk in and was no longer directly exposed on the outside of the head. It is formed by a groove between the outer edge of the tabulare and the squamosal; this groove terminates suddenly where the tabulare ends in a definite projection from the back of the skull which must mark the upper insertion of the membrane.

It is known from the evidence of specimens which show the complete stapes in position—*Eryops*, *Trimerorachis*, *Cyclotosaurus*, etc.—that in Stegocephalia the tympanic membrane was stretched between the tabulare and the squamosal across the otic notch on the upper surface of the skull. By direct tracing back of homologous parts we have seen that in Deinocephalia the upper end of the membrane should be attached to the squamosal and the extreme distal end of the tabulare: that is, in the exact position we know it to have been attached in Stegocephalia related, although remotely, to the Deinocephalian's amphibian ancestors.

It will be convenient here to leave this particular line of argument, and starting from the normal conditions of the membrana tympani in Reptiles, try to reconstruct the arrangement in *Dimetrodon*, and so work back to the termination of our original argument at the Deinocephalia.

In Lizards the insertion of the tympanic membrane is on to the back of the quadrate, the squamosal just outside the paroccipital process, and the retro-articular portion of the lower jaw.

In Pelycosaurs and other Therapsids the retro-articular portion of the lower jaw is of insignificant proportions, at its largest in *Dimetrodon*. In Deinocephalia and *Dicynodon* it is represented solely by a small process from the articular directed as much downwards as backwards. The definite presence of this process in these more primitive forms and its still further reduction in later types, seem to show that some Therapsid ancestor had a relatively large retro-articular process. As in all reptiles which have such a process its outer side is covered by the angular, we may assume that in this hypothetical ancestral Therapsid the retro-articular portion of the angular played some part in the support of the tympanic membrane. If now in such an animal we make the tubo-tympanal cavity grow forwards and the membrane to keep pace with it in such change, we must also move forward the upper edge of the retro-articular part of the angular to which the membrane is attached. As it is essential to keep the stretched membrane clear of other bones, and the articular and quadrate are by hypothesis fixed, we can only do so by separating the edge of the retro-articular part of the angular from other bones and moving it slightly outwards: this on the theory which I am at present expounding is the origin of the Therapsid notch, the upper edge of the reflected lamina being phylogenetically the upper border of the retro-articular portion of the angular, and retaining that connection with the lower edge of the membrana tympani which occurs in Lizards. By this method we arrive at a position of the tympanic membrane in Deinocephalia identical with that deduced by tracing the conditions down from Cynognathids, the arrangement in which was determined by assuming that the great resemblance between the angular of these types, with their long, slender, downwardly directed "reflected lamina," and the tympanic of a pouch-young of *Perameles* with its slender lower limb, was a real one. The fact that it is possible to trace a sequence of stages with only very few hypothetical intermediates between the actual condition of the membrana tympani in lizards and that in embryo mammals, and that these stages are in the correct time order, and are each self-consistent, seems to me to establish a probability that the assumption on which they depend, *i. e.* that the reflected lamina of the Therapsid angular carried the tympanic membrane, is a justifiable one.

I am quite aware that the shape of the edge of this lamina in some types, as for example in *Endothiodon* and Anomodonts generally, is inconsistent with the view that it carried the membrane, but as in all these types the squamosal never shows any suggestion of an auditory groove or of the attachment of a membrane, I think it possible that they were without one, a not unknown condition.

In 1910 W. K. Gregory, from the position of the auditory groove in *Cynognathus*, inferred that the tympanic cavity and membrane were below the reduced quadrate and articular. From these relations and the fact that in the ontogeny of a mammal the tubo-tympanal cavity grows up round the auditory ossicles which arise outside it, he suggested that phylogenetically this upgrowing of the tubo-tympanal sac around the vestigial quadrate and articulare may have caused them to share in its vibrations, and thus to take on an incipient auditory function before their old suspensory function had ceased.

This is exactly the conclusion to which the above discussion, founded mainly on quite different evidence, has led us.

In mammals the centre of the tympanic membrane is placed in connection with the chain of auditory ossicles by the handle of the malleus being fastened to its middle layer. In no Therapsid that I have yet examined is there a process of the articulare which could touch the membrane, so that it is inherently probable that the manubrium is a mammalian innovation. In ontogeny it arises very late, chondrifying much later than the incus and body of the malleus in *Perameles*, but being apparently a real part of the latter bone.

It thus seems impossible that the membrane of Therapsids should be brought into connection with the fenestra ovalis in the ordinary mammalian way, and as the whole of the preceding arguments are meaningless if they have no membrane, it seems certain that another connection between the stapes and the membrane must have existed.

In a remarkably able and suggestive paper, Dr. Gregory has put forward the following explanation :—

"That in the most primitive Cynodonts, such as *Bauria*, there was an extra-columella, resting against a tympanic membrane behind the squamosal, which had been differentiated out of the tissue lying between the endodermal epithelium of the tympanic cavity and the epidermis : that with the spread of the tympanic cavity the differentiation of the future tympanic membrane also spread, until it included the stretched skin on the posterior end of the jaw below the quadrate and articular and above the angular : that concomitantly with the reduction of the quadrate and articular and the detachment of the angular and goniale from the dentary, the newly differentiated portion of the tympanic membrane became functionally more active than the old 'reptilian' portion : that in this way the old membrane together with the extra-columella became vestigial, while the new membrane became altogether free from the dentary, but remained fastened both to the angular, which gave rise to the tympanic bone, and to the retro-articular process of the articular, which gave rise to the manubrium of the malleus. With the reduction of the 'reptilian' tympanic membrane the hyoid became separated from the extra-columella (as it does in many lizards) and migrated to a new insertion on the periotic."

The foregoing discussion will have shown how much of truth there may be in this brilliant hypothesis of Gregory's. The suggestion that the stapes of Therapsids although directly articulated with the quadrate may have been connected with the membrane by an extra-columella, is exactly paralleled by the actual conditions in Mosasaurs, where the slender stapes is inserted into a deep pit on the inner side of the quadrate, but is connected with the tympanic membrane by a process passing through the large special notch on the back of that bone. This process like the membrane is sometimes strongly calcified. The whole arrangement is after all only a further development of conditions commonly found in lizards.

The facts as we know them in *Diademodon*, or rather the interpretations of those facts offered above, show that the reptilian portion of the tympanic membrane had actually been reduced to very small dimensions by a steady process connected with and no doubt induced by the same factor as the degeneration of the quadrate and the thinning of the basisphenoid and basioccipital.

The facts also seem to show that the manubrium mallei is altogether a new formation, developed whilst the articular was losing its suspensory function.

If the explanation of the meaning of the observed series of changes in the articular region of the skull of Therapsids which has been presented above be true, or even if it contains but a small element of truth, it presents us with a good illustration of the fact, to my mind patent in the development of every organ of the body which is known, that the Therapsids from the moment of their initiation were committed to the final development of a mammalian structure. Different branches of them proceeded with their modifications to different degrees, and at very different speeds, but so far as the evidence goes, and it is no more than suggestive at best, their evolutionary change, in fundamental features, were always directed towards the final development of a mammalian structure.

I wish to acknowledge my indebtedness to the Percy Sladen Trustees, who assisted me in visiting the South African Museums. To Dr. Smith Woodward I owe the opportunity of describing the material in the British Museum (Natural History), which is the basis of this paper, and I also owe to him and to Dr. C. W. Andrews thanks for their many kindnesses during my work at the Museum. Finally, I have to thank Mr. R. Hall, chief "mason" at the Museum, who developed the skulls described in this paper from a matrix which in many places is as hard as flint.

EXPLANATION OF THE PLATES.

Plate IV.

Fig. 1. Skull of *Mormosaurus seeleyi*, gen. et sp. n. Type specimen (R. 3594). From side. About $\frac{1}{6}$ nat. size.

Fig. 2. Skull of *Mormosaurus seeleyi*, gen. et sp. n. Type specimen (R. 3594). Obliquely from front. About $\frac{1}{6}$ nat. size.

Plate V.

Skull of *Titanosuchus ferox* Owen. (R. 3595.) From above. About $\frac{1}{3}$ nat. size.